

Biogeographic area relationships of Cuba with the rest of the Neotropical region based on the distributions of genus *Gochnatia* KUNTH

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Abstract

Hypotheses of the historic biogeography of Neotropical *Gochnatia* were generated using Parsimony Analysis of Endemicity. Cladistic analysis of the distribution of 38 *Gochnatia* species at 11 areas showed two regions that form a basal dichotomy: (I) South Bolivia + Northwestern Argentina and (II) Caribbean Region + Amazonian Peru + Brazilian Atlantic Forest. The application of a cladistic analysis to the biogeographical information gathered, enabled us to establish relations among the several distribution areas of *Gochnatia* section *Gochnatia* and also allowed us to represent the graphical confirmation of the existing, unmistakable disjunction within this genus.

Introduction

The genus *Gochnatia* KUNTH, placed by all synantherologists in the tribe Mutisieae subtribe Mutisiinae, is a challenging subject for researchers due to its 68 species and disjunct geographic distribution. Current knowledge shows it has two Paleotropical species in Southeast Asia from Northern India to Laos and Vietnam, whereas most species are found in the Neotropics and in the south of the United States of America. *Gochnatia* was first described by KUNTH in "Nova Genera and Species Plantarum" (1818), the type species being *Gochnatia veronioides* KUNTH from Peru.

Several taxonomic treatments, either considering two, three or five sections, have been applied to the genus. Among the studies on the family (and to a certain extent on *Gochnatia*) during the 19th century, those of CASSINI (1824), LESSING (1830, 1832), DE CANDOLLE (1836) and BENTHAM & HOOKER (1873) are classics.

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During the 20th century, the most complete papers including many innovations and changes are those of ANGEL CABRERA (1971) and an unpublished thesis by ROY N. JERVIS (1954); the latter made a study of the genus with strong emphasis on Caribbean species, which up to that time had been included in the genus *Anastrophia* D. DON. CABRERA (1971) published a monograph of the genus proposing the infrageneric classification currently accepted (6 sections and 68 species):

- Sect. I. *Gochnatia*: 38 species; 30 in the Caribbean and 8 in South America.
- Sect. II. *Pentaphorus*: 2 species in South America.
- Sect. III. *Moquiniastrium*: 18 species in South America.
- Sect. IV. *Leucomeris*: 2 species in East Asia.
- Sect. V. *Hedraiophyllum*: 7 species in North America.
- Sect. VI. *Discoseris*: 3 species in Brazil.

There are 30 Caribbean and eight South American species in Section *Gochnatia*. They are monoecious shrubs or small trees; capitula solitary or in small number, sessile at the end of branches.

Section *Gochnatia* has three disjunct areas of distribution:

1. Thirty species are endemic to the Bahamas and the Greater Antilles, mainly in Cuba, a few in the Haiti and the Dominican Republic.
2. Seven species are scattered all along the eastern slopes and intermountain valleys of the Andes from northern Peru to northwestern Argentina.
3. A single species is endemic to southeastern Brazil.

The present investigation analyses the distributional patterns of Neotropical *Gochnatia* by cladistic parsimony techniques. The purpose of this analysis is to generate hypotheses of the historical biogeography of the group.

Materials and Methods

A technique that uses cladistic parsimony to infer historic relationships among areas is Parsimony Analysis of Endemicity (PAE). This procedure, proposed by ROSEN (1988) and ROSEN & SMITH (1988), has been applied increasingly in several biogeographic studies to a variety of taxa and regions.

PAE was applied to the distribution of 38 species of *Gochnatia* in 11 areas of Neotropical regions in the Caribbean Region and South America (Table 1). The circumscriptions of the areas sampled were defined by the present authors (Fig.1).

For the PAE, the presence or absence of species was coded in a matrix of taxa versus areas (0 for absence, 1 for presence). A hypothetical "empty locality"(RA) where no

species occur was used to root area cladograms (ROSEN 1988, CRACRAFT 1991).

The analysis was carried out using the program WINCLADA vers. 0.9.9 (NIXON 1999) and applying heuristic methods for searching, implicit in the program. The reliability of results was determined by means of consistency (CI) and retention (RI) indices also implicit in the program calculations.

Results were compared to the available information on the paleogeography of the area.

Results and Discussion

One most parsimonious area cladogram (CI = 100, RI = 100, tree length = 38) was obtained (Fig. 1) from cladistic analysis on the distribution of 38 *Gochnatia* species at 11 areas. Two regions form a basal dichotomy: (I) South Bolivia + Northwestern Argentina and (II) Caribbean Region + Amazonian Peru + Brazilian Atlantic Forest.

The topology of this cladogram (Fig. 1) reveals the existence of a large group (II), where the Caribbean Region is divided in two subgroups: IIa and IIb2. Subgroup IIa is supported by *Gochnatia microcephala* var. *buchii* (9), *Gochnatia microcephala* var. *rosei* (10), *Gochnatia oligantha* (13) and *Gochnatia sessilis* (15), all of which are widely distributed in Hispaniola. In that island there are eight species, three of which are endemic to Haiti and only one is endemic to the Dominican Republic.

The Subgroup IIb2 is supported by *Gochnatia ilicifolia* (17), a species widely distributed in Cuba and also found in some islands of the Bahamas. It all seems to point at a Cuban origin followed by further dispersal into the Bahamas. In this subgroup, four distinctive clusters were defined and represent Cuban floristic sectors sensu SAMEK (1973), having a large number of endemics, and the Bahamas with just a single endemic, *Gochnatia pauciflorescens* (18).

In regard to Cuban species, there is a center of diversification in each Cuban phytogeographic sector. The western and central centers are very related and have 4 endemics each: *Gochnatia mantuensis* (20), *Gochnatia ekmanii* (24), *Gochnatia montana* (26) and *Gochnatia intertexta* (29) in Western Cuba, and *Gochnatia sagraeana* (22), *Gochnatia wilsonii* (25), *Gochnatia cowellii* (28) and *Gochnatia parvifolia* (32) in Central Cuba. However, the most important center of diversification is in Eastern Cuba, which is the sister area of the rest of the clade and has 12 endemics (60 % of all Cuban endemic species of *Gochnatia*). This result agrees with those of other workers recognizing Eastern Cuba as the most endemic-rich sector.

The high percentage of endemism is a natural consequence of various factors including environmental heterogeneity and wide diversity of habitats and soils which

are traits inherent to islands, opposing the characteristic homogeneity of continents.

Ecological vicariance among the species of *Gochnatia* is another interesting aspect: ten are restricted to limestone, nine thrive on serpentine habitats exclusively and only one is able to live in the white sand of Pinar del Río, *Gochnatia mantuensis* (20). Analysis of dispersal patterns of each of these ecologic groups shows a total coincidence with the dispersal patterns of limestone and serpentine floras (BORHIDI 1991, 1996).

According to BORHIDI's patterns, limestone vegetation had its primary evolution centers in Pinar del Río (Western Cuba) and in the mountains of Eastern Cuba. In both centers *Gochnatia* has characteristic species such as *Gochnatia ekmanii* (24) and *Gochnatia montana* (26) in Pinar del Río and *Gochnatia microcephala* var. *microcephala* (11), *Gochnatia elliptica* (27), *Gochnatia calcicola* (30), *Gochnatia maisiana* var. *maisiana* (33) and *Gochnatia maisiana* var. *parviflora* (34) in Eastern limestones.

Centers of evolution on serpentine are the Nipe-Sagua-Baracoa mountains (eight species), Moa being the primary center and Nipe the secondary one. Species have migrated from Eastern to Western Cuba along the serpentine axis (Holguín-Guanabacoa). Species restricted to serpentine can be found in almost every serpentine area from Baracoa (easternmost Cuba) to Pinar del Río (westernmost Cuba) where the Cajalbana mountains are a terciary evolution center. *Gochnatia intertexta* (29) is the westernmost species of *Gochnatia* in Cuba that lives in serpentine soil.

The species of *Gochnatia* have evolved in old rocky limestone and serpentines, at an altitude of 0-1000 m though the limit is 1250 m in Sierra Cristal (Eastern Cuba). They thrive in the following vegetation units: 1) littoral dry scrub, 2) dry evergreen forest, 3) humid evergreen forest, 4) rainforest, 5) thorny dry scrub on serpentine, 6) subthorny dry scrub on serpentine, 7) mountain scrub and 8) semideciduous forest. They can sometimes be found in gallery forest in the above mentioned units.

On the other hand, in Subgroup IIb one clade is formed by the Bolivian center and Brazilian Atlantic Forest. Both of them appear in the cladogram as a unique unit but they do not have any species in common, the two areas only presenting strictly endemic species.

Peru is an independent area belonging to the Subgroup II. It has a considerable percentage of endemism and its taxa are not shared with any other region.

Subgroup I supported by *Gochnatia curviflora* (4) joined two areas, viz., South Bolivia and Northwestern Argentina.

This high endemism in continental species might be due to the isolation of South America during nearly all of the Cenozoic. The elevation of the Andes as a geographic

barrier between lowland forests has been decisive for the patterns of endemism of Neotropical forest (RON 2000); also, the extreme ecological conditions under which the species live. Most of them are high mountain dwellers, found above 2000 m, where the climate is hard and forces them to create adaptative mechanisms, which ultimately restrict their distribution areas.

According to our cladogram, it is obvious that continental (I, IIb and an independent area) and insular (IIa and IIb2) groups are well defined and in general the biotic and abiotic conditions are important forces determining the distribution of *Gochnatia* species in the Neotropics.

Biogeographical considerations in *Gochnatia* resulting from available information on the paleogeography of the area

The genus *Gochnatia* and section *Gochnatia* have a disjunct geographical distribution (Fig.2). There are eight continental species restricted to South America and 30 species in the Greater Antilles and the Bahamas. BORHIDI (1991, 1996) claimed that the origin of the genus is Gondwanian with Andean species playing a leading role. *Gochnatia* was first thought to have originated in the Northern Andes with subsequent dispersal along the Pacific coast and Beringia and a Neogene arrival to Paleotropical Asia. However, BREMER (1994) suggests that it could have arisen in the whole Pacific area during the Oligocene. Likewise, the lack of species in the Holarctic tends to imply that they became extinct during the Miocene-Pleistocene climatic changes, that is, Northernmost American and Northeastern Asiatic species disappeared during the Late Tertiary and Early Quaternary, thus rendering the present disjunct tropical distribution of the genus.

The disjunct distribution of *Gochnatia* section *Gochnatia* can be assessed on the ground of the Cuban floristic evolution (BORHIDI 1996). According to this hypothesis there were three phases: 1) The plate phase between the Upper Jurassic and Early Cretaceous when the Antillean plate was located to the north of the African and South American continents, having contact with the Macaronesian plate and hence receiving floristic influence from the Pacific coasts. However, there is no evidence of the existence of Asteraceae in those Mesozoic periods. 2) The land-bridge phase between the Eocene and the Pliocene when *Gochnatia* had already arisen in the Pacific area and had all the conditions for further dispersal from the continent to the Greater Antilles. Though not continuous, this phase has the greatest probability of being the time during which *Gochnatia* arrived to the Macroantilles since these islands had a direct connection with South America via Andes-Aves crests, and Central America-Nicaragua and Cayman crests. 3) During the archipelago phase the connections between the islands and the continents ceased and isolation among the

Greater Antilles began to increase, thus contributing to the formation of endemic species.

Conclusions

- The continental (I, I1b1) and insular (IIa, I1b2) groups are well defined in the cladogram.
- Topology in the cladogram shows that the closest relations and affinities are those between the Bahamas and Cuban areas and between the Haiti and Dominican Republic areas.
- The Western Cuba and Central Cuba centers are closely related and have 4 endemics each.
- The Eastern Cuba center (12 endemics) is the most important source of diversification within the Cuban archipelago.
- Cuba and Hispaniola are centers of evolution of *Gochnatia* in the Greater Antilles.
- The genus *Gochnatia* and Section *Gochnatia* have a disjunct geographical distribution between the Greater Antilles and Central Western South America (though one taxon is found in Southeastern Brazil).
- The biotic and abiotic conditions are important forces determining the distribution of *Gochnatia* species in the Neotropics.

Acknowledgements

We are grateful to PEDRO PABLO HERRERA OLIVER of the Ecology and Systematics Institute for revising the English text, to HERIBERTO RODRIGUEZ for drawing of figure and to BERTIL NORDENSTAM for the critical review of the manuscript. We also want to thank the Department of Phanerogamic Botany at the Swedish Museum of Natural History and the Swedish Institute for supporting these studies.

Table 1. Species of *Gochnatia* in the cladogram. No. = number of a species in the tree.

Species	No.	Species	No.
<i>G. rotundifolia</i> LESS.	0	<i>G. recurva</i> (BRITT.) JERVIS et ALAIN	19
<i>G. cardenasi</i> S. F. BLAKE	1	<i>G. mantuensis</i> (WRIGHT ex GRISEB.) JERVIS et ALAIN	20
<i>G. arequipensis</i> SANDWICH	2	<i>G. attenuata</i> (BRITT.) JERVIS et ALAIN	21
<i>G. vargasi</i> CABRERA	3	<i>G. sagraeana</i> JERVIS et ALAIN	22
<i>G. curviflora</i> (GRISEB.) HOFFM.	4	<i>G. crassifolia</i> (BRITT.) JERVIS et ALAIN	23
<i>G. boliviana</i> S.F. BLAKE	5	<i>G. ekmanii</i> (URB.) JERVIS et ALAIN	24
<i>G. vernonioides</i> KUNTH	6	<i>G. cowelli</i> (BRITT.) JERVIS et ALAIN	25
<i>G. patazina</i> CABRERA	7	<i>G. montana</i> (BRITT.) JERVIS et ALAIN	26
<i>G. enneantha</i> (BLAKE) ALAIN	8	<i>G. elliptica</i> (LEÓN) ALAIN	27
<i>G. microcephala</i> var. <i>buchii</i> (URB.) ALAIN	9	<i>G. wilsonii</i> (BRITT.) JERVIS et ALAIN	28
<i>G. microcephala</i> var. <i>rosei</i> (BRITT.) ALAIN	10	<i>G. intertexta</i> (WRIGHT ex GRISEB.) JERVIS et ALAIN	29
<i>G. microcephala</i> (GRISEB.) JERVIS et ALAIN var. <i>microcephala</i>	11	<i>G. calcicola</i> (BRITT.) JERVIS et ALAIN	30
<i>G. obovata</i> (URB. et EKM.) JIMÉNEZ	12	<i>G. gomezii</i> (LEÓN) JERVIS et ALAIN	31
<i>G. oligantha</i> (URB.) HOWARD	13	<i>G. parvifolia</i> (BRITT.) JERVIS et ALAIN	32
<i>G. picardae</i> (URB.) JIMÉNEZ	14	<i>G. maisiana</i> (LEÓN) JERVIS et ALAIN	33
<i>G. sessilis</i> ALAIN	15	<i>G. maisiana</i> var. <i>parviflora</i> (LEÓN) ALAIN	34
<i>G. tortuensis</i> (URB.) JIMÉNEZ	16	<i>G. cubensis</i> (CARABIA) JERVIS et ALAIN	35
<i>G. ilicifolia</i> LESS.	17	<i>G. obtusifolia</i> (BRITT.) JERVIS et ALAIN	36
<i>G. pauciflosculosa</i> (WRIGHT ex HITCHC.) JERVIS ex CABRERA	18	<i>G. shaferi</i> (BRITT.) JERVIS et ALAIN	37

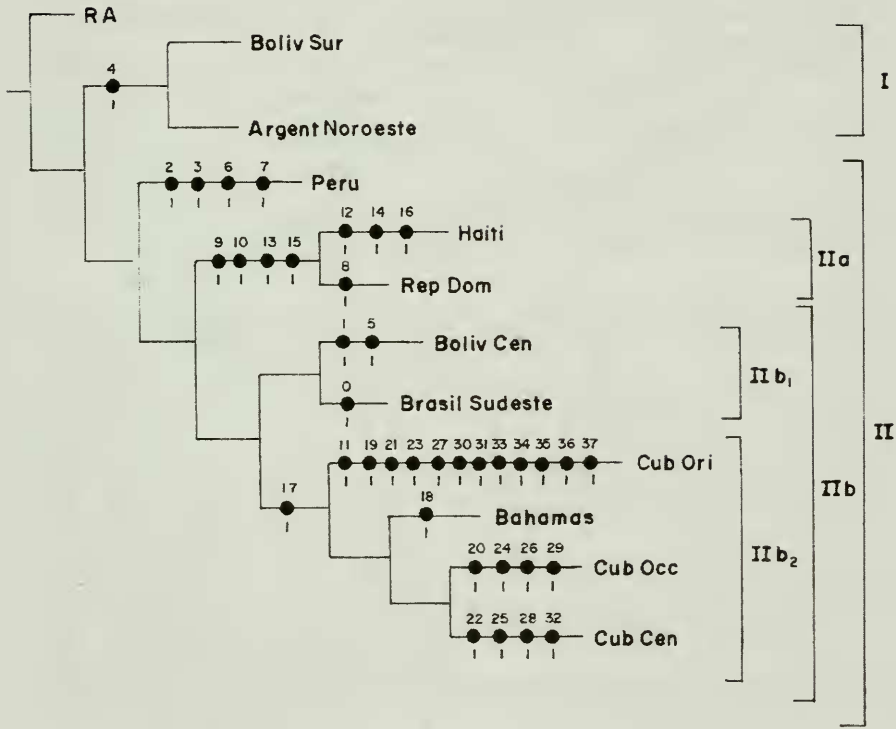


Fig. 1. Most parsimonious area cladogram (tree length = 38, CI = 100, RI = 100) for Parsimony Analysis of Endemicity applied to presence/absence of 38 species of *Gochnatia* at 11 areas. An empty locality (no species) was used to root the cladogram (RA).

• Existence of taxa; the number above the dot is the taxon's number.

BolivSur: South Bolivia; ArgentNoroeste: Northwestern Argentina; RepDom: Dominican Republic; BolivCen: Central Bolivia; CubCen: Central Cuba; CubOcc: Western Cuba; CubOri: Eastern Cuba.

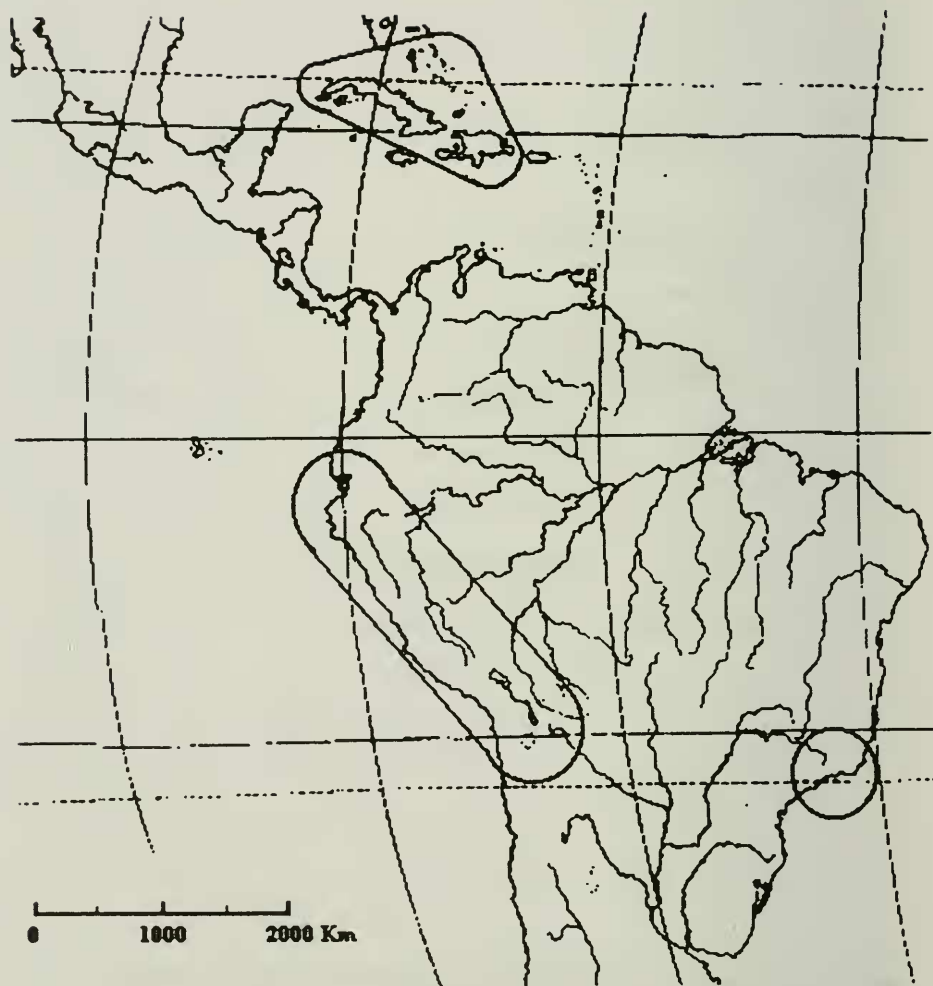


Fig. 2. The disjunct geographical distribution of *Gochnatia*, section *Gochnatia*.

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